SONG VARIATION IN A POPULATION OF MEXICAN JUNCOS

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The variability of bird songs is familiar to all field ornithologists. Geographical variation in particular has received considerable attention partly for its intrinsic interest and partly because its understanding promises to throw some light on the role of reproductive isolating mechanisms in speciation.

However, the problem of describing geographical variation in song is complicated by the excessive variability which we sometimes find within a single population of birds, as in the European Chaffinch, *Fringilla coelebs* (Marler, 1952). An understanding of the extent and significance of this local variation is a prerequisite for analysis on a geographical scale. During an expedition to Mexico in 1958 an ideal opportunity was found for such study in the pine woodlands near El Salto in Durango. Mexican Juncos (*Junco phaeonotus*) are very common there, and the habitat is uniform. It was possible to record songs from a large number of males—67 songs in all from 63 males—within a restricted area of about one square mile. This sample of songs from a single population is much more variable than in other species we have studied such as the Chipping Sparrow and the Brown Towhee (Marler and Isaac, 1960*a*, *b*). Our intention in this paper is to try to document this variation, both in terms of the over-all characteristics of the song and also with regard to the structure of the component syllables. We thus hope to determine which characteristics persist throughout this variability, providing the basis for whatever species-specific properties the song of the Mexican Junco may have.

METHODS

The songs were recorded in the field with a Magnemite 610 E tape recorder at a tape speed of 15 inches per second with an Altec 633A microphone mounted in a parabolic reflector. A Madison Fielding Micamp was used in the microphone circuit. In the laboratory the tapes were played back on a Viking 75 tape deck modified to operate with a tape speed of 15 inches per second. Analyses were made with a Kay Electric Company Sonagraph and amplitude display unit using the wide band-pass filters and the "high-shape" setting in all cases. The syllable analyses are based on ink tracings made directly from the sonagrams on tracing paper. Figures 1 and 6 are from photographs of tracings of this kind. The recordings were made between 29 June and 3 July 1958, within an area of approximately one square mile within short walking distance of a camp in the pine forests to the northwest of El Salto, in Durango, Mexico. Two or three examples of the songs of each bird were recorded. From each of these samples one example of each song

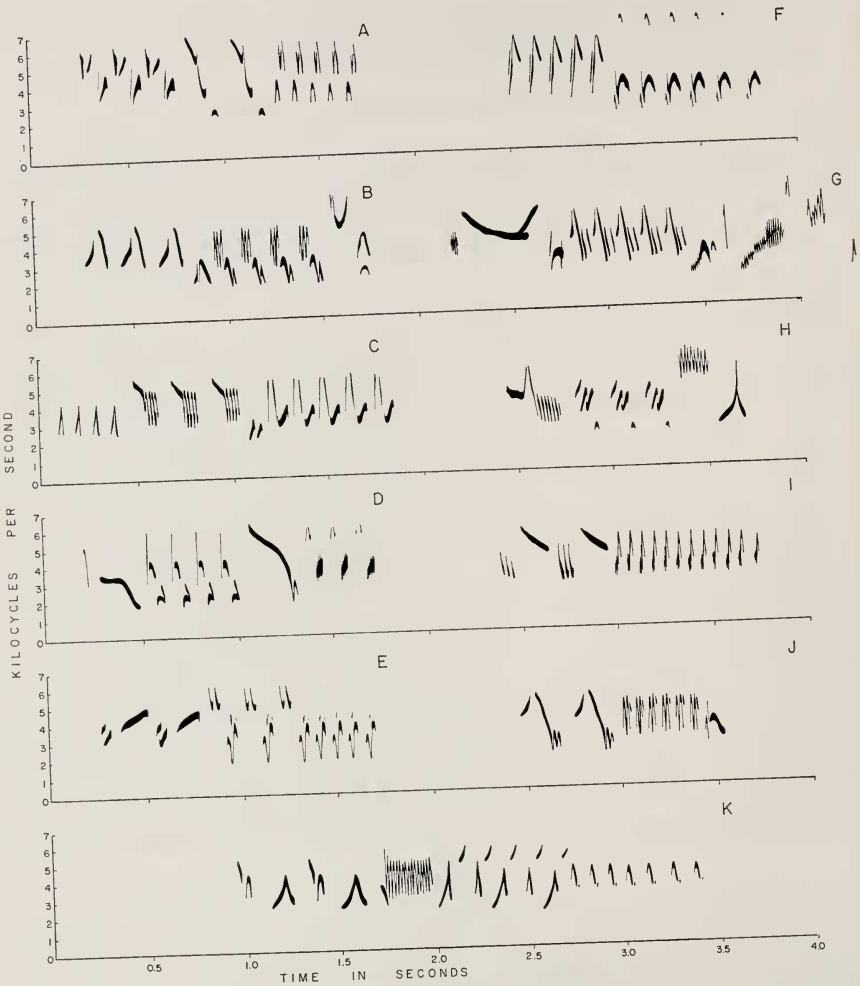

FIG. 1. Sonagrams of songs of 11 individuals selected from recordings made near El Salto, Durango. A–E: These songs represent the most common condition (based on such characteristics as over-all duration, number of syllable types per song, number of trills per song, etc.). F–K: These songs represent extremes as follows: F—few syllable types; G—many syllable types; H—few trill syllables; I—many trill syllables; J—a short song; K—a long song.

pattern recorded was selected for analysis. Data on the frequency and temporal characteristics of the songs were read off on a graduated clip board (see Marler and Isaac, 1960*a*). Unless otherwise stated, the data are presented as arithmetic means plus or minus one standard deviation.

TABLE 1

FREQUENCY OF DIFFERENT TYPES OF SONG, CLASSIFIED ACCORDING TO POSITION AND NUMBER OF TRILLS AND PHRASES*

One-trill songs		Two-trill songs		Three-trill songs		
4	aBc	13	AB	5	ABC	
3	Ab	12	ABc	2	AbCD	
		9	AbC	2	ABCd	
		7	AbCd	1	ABcD	
		4	aBC	1	AbCDe	
		2	aBcD	1	ABcDe	
		1	aBCd			
Totals	7	48		12		67

* Trills are represented by capital letters, and phrases by small letters.

GENERAL DESCRIPTION OF THE SONG PATTERN

In a sustained bout of singing, a bird delivers one pattern several times with little variation, then switches to another and then returns to the first, and so on. In most cases we have recorded only one song pattern from each bird. Mexican Juncos have a complex song, considerably more elaborate than the simple trill of the Oregon or Slate-colored Juncos. Although the song is about the same duration as in other juncos, it is built from several syllable types instead of just one. Each male has a repertoire of several song patterns, two or three being an average estimate from field observations.

Song analyses of this sort pose a problem in terminology. For sake of clarity in the following descriptions and discussions we have used the terms *note*, *syllable*, *trill*, and *phrase*. These terms are useful in this particular case, but may not have any general application. In fact it may be difficult or even impossible to use the same terminology for other types of songs, such as those of some of the more versatile singers (thrushes, etc.). Until such songs are analyzed and a suitable terminology derived, the terms used herein should not be extended beyond their present context.

In the terminology we use for the different parts of the song, as revealed in a sonagram, the basic units are the *notes*, each of which is one continuous vocal utterance. A single note may be modulated in frequency or amplitude in a complicated way, to form quite an elaborate unit. Any break in continuity is regarded as the end of a note. Notes are often arranged in groups to form more or less coherent units, which are the *syllables*. These are not always easy to identify with certainty, except when they are repeated consecutively two or more times, to make a *trill*. When they are not repeated in this fashion, their identification becomes more arbitrary (although the term is still useful).

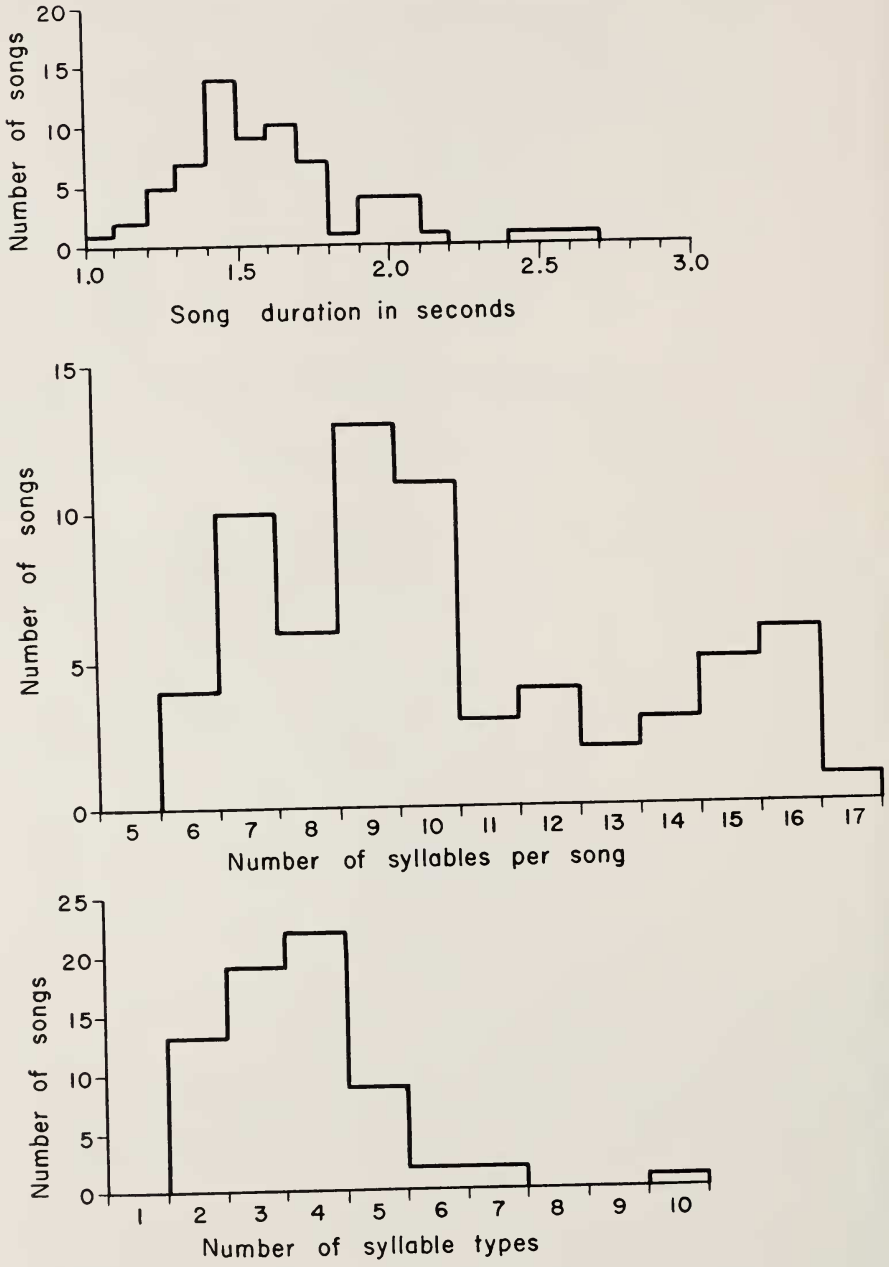

FIG. 2. Frequency distributions of song duration, number of syllables per song, and number of syllable types per song.

Our final subdivision is a *phrase*, one or more such unrepeated, dissimilar syllables which, in these songs, are separated from other phrases by a trill. Using these subdivisions we can make a complete description of the song, beginning with its over-all characteristics, then proceeding to a finer analysis of the structure of individual syllables and notes.

On careful examination we can discern some patterning in the ways in which the syllables are arranged in the songs of different birds. Each song always includes one or more trills. In a few cases there is only one trill sequence (e.g., Fig. 1H), usually two (Fig. 1B), and occasionally three (Fig. 1A). These trills are arranged in many varied ways. The song may begin with a trill (Figs. 1A, B, etc.) or with a phrase (Figs. 1D, G, etc.). Two trills may follow immediately on each other or may be separated by a phrase. And the song may or may not terminate with a trill. The majority of the songs (49) had at least one phrase. Table 1 shows that the number of basic parts in the song can vary through two (16 songs), three (34 songs), four (15 songs), and five parts (2 songs).

The average duration of all songs (Fig. 2) was 1.63 ± 0.29 seconds. Thirty-five unbroken pauses between consecutive songs in the recordings averaged 5.4 ± 1.4 seconds. Thus, at a rough estimate, these birds spend about 23 per cent of their singing time actually in song. The number of syllables in the song also varies, from 6 to 17, with an average of 10.1 ± 2.9 (Fig. 2). In neither respect is this variability excessive, as compared with the Brown Towhee, in which song duration varies similarly, and the number of syllables per song is considerably more variable (10.4 ± 4.5, Marler and Isaac, 1960*b*). As in the towhee, there is a rough correlation between these two measures, shorter songs tending to have fewer syllables than longer ones, but there are many exceptions. One song with 6 syllables, for example, was longer than another with 14 syllables.

There is also a diversity of syllable types in each song (Fig. 2) but the number per song, 3.7 ± 1.4 is relatively consistent. Thus, each song always has at least two syllable types, and rarely has more than five. As pointed out earlier, some of these are given only once in a song, while others are repeated. We can express the amount of repetition in the ratio of the number of syllables to the number of syllable types (Fig. 3). For this sample the value is 2.97 ± 1.05. This is a much lower figure than we would obtain for the Chipping Sparrow or the Brown Towhee, but, nevertheless, the trills are a prominent characteristic of Mexican Junco songs, and merit closer attention. The trills make up the greater proportion of each song, contributing 8.5 ± 2.7 syllables and a duration of 1.24 ± 0.29 seconds, as compared with 0.40 ± 0.25 seconds from 1.7 ± 0.9 phrase syllables. The lower variability of the figures on trills, particularly the duration, emphasizes their importance as a basic characteristic of the song, as compared with the less regular phrases.

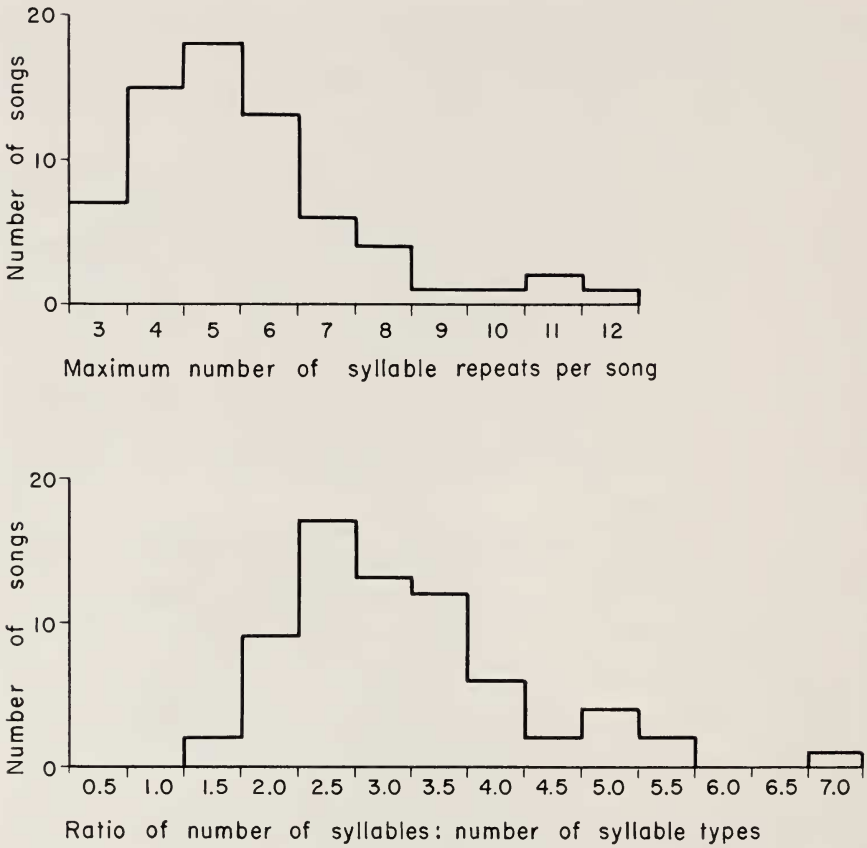

Fig. 3. Frequency distributions of maximum number of syllable repeats per song, and ratio of number of syllables to number of syllable types per song.

An estimate of the number of syllables which make up a trill can be obtained from the maximum number of consecutively repeated syllables in each song (Fig. 3). If we summarize the number of syllables in all of the trills in all songs the average number of syllables per trill is 4.1 ± 2.0, as compared with 1.7 ± 0.9 phrase syllables. The duration of syllables is similar in trills (0.138 ± 0.077 sec) and in phrases (0.135 ± 0.097 sec), the average figures for the songs as a whole being 0.137 ± 0.087 second. In phrases this duration is not related to the number of syllables present. In trills the two characteristics are correlated in an inverse fashion. the trills with most syllables having the shortest syllables. In those with two syllables, the average duration is 0.225 second per syllable; in those with three, 0.158 second; with four, 0.105 second; and so on, down to 0.050 second with

TABLE 2

SUMMARY OF DATA DISCUSSED COMPARATIVELY IN TEXT WITH ADDITION OF STANDARD ERRORS AND 95% CONFIDENCE INTERVALS*

	N	$\bar{X}$	s	$s_{\bar{x}}$	Confidence interval $p = 0.05$
Number of syllables per trill	139	4.1	± 2.0	± 0.17	± 0.33
Number of syllables per phrase	65	1.7	± 0.9	± 0.11	± 0.22
Trill syllable duration in seconds	138	0.138	± 0.077	± 0.0066	± 0.0129
Phrase syllable duration in seconds	111	0.135	± 0.097	± 0.0092	± 0.0182
Trill syllable duration in seconds by number of syllables per trill					
2-syllable trills	34	0.225	± 0.063	± 0.0108	± 0.0220
3-syllable trills	32	0.158	± 0.056	± 0.0098	± 0.0200
4-syllable trills	22	0.105	± 0.061	± 0.0130	± 0.0269
>4-syllable trills	446	0.085	± 0.033	± 0.0049	± 0.0100
Number of syllables per trill by position in song					
First trill	67	3.5	± 1.7	± 0.21	± 0.42
Other trills	72	4.6	± 2.2	± 0.26	± 0.52
Duration in seconds of trills by position in song					
First trill	67	0.67	± 0.16	± 0.020	± 0.040
Other trills	70	0.55	± 0.19	± 0.023	± 0.046
Duration in seconds of trill syllables by position in song					
First position	56	0.188	± 0.073	± 0.0097	± 0.0194
Second position	45	0.103	± 0.055	± 0.0082	± 0.0166
Third position	30	0.105	± 0.074	± 0.0135	± 0.0275
Fourth and Fifth positions	7	0.103	———	———	———
Note types by number of notes per syllable					
Vibrato notes	117	2.0	± 0.8	± 0.07	± 0.14
Non-vibrato notes	378	2.7	± 1.2	± 0.06	± 0.12
Number of notes per syllable					
Trill syllables	138	2.4	± 1.1	± 0.09	± 0.18
Phrase syllables	108	1.5	± 0.8	± 0.07	± 0.15

* N is the sample size; $\bar{X}$, the arithmetic mean; s, the standard deviation of the sample; and $S_{\bar{x}}$, the standard error of the mean. Symbols and calculations are based on Simpson, Roe, and Lewontin (1960).

eight syllables. The differences between two-, three-, and four-syllable trills are the only ones which are statistically significant (Table 2). The same relationship has been described in the trills of the Brown Towhee song (Marler and Isaac, 1960*b*).

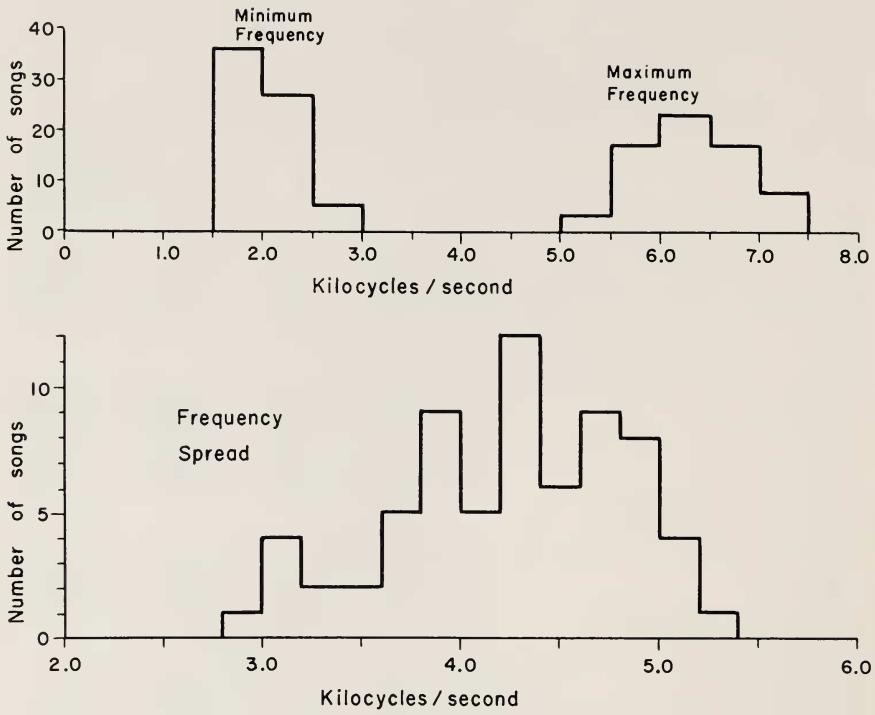

FIG. 4. Distributions of maximum and minimum frequencies per song, and frequency spread per song.

FREQUENCY CHARACTERISTICS

As in the songs of the Chipping Sparrow and the Brown Towhee, the frequency characteristics vary widely (Fig. 4). Once again, the minimum frequency (2.09 ± 0.25 kilocycles per second) is less variable than the maximum (6.39 ± 0.51 kc). The frequency spread which a song may span ranges from 3.0 to 5.4 kc (average 4.30 ± 0.58 kc).

TRENDS THROUGH THE SONG

Thus far we have established certain basic characteristics of Mexican Junco song; its duration, and the number of syllable types, the presence of phrases and of trills. Next we must look for any systematic changes in the course of the song. First, we could find no systematic changes in loudness through the song, as seen in amplitude displays of selected song patterns. In some cases the earlier syllables have the highest amplitude, in other cases, the loudest ones are later in the song. Within a trill the amplitude of the syllables is the same. The position of the trills in the song has already been

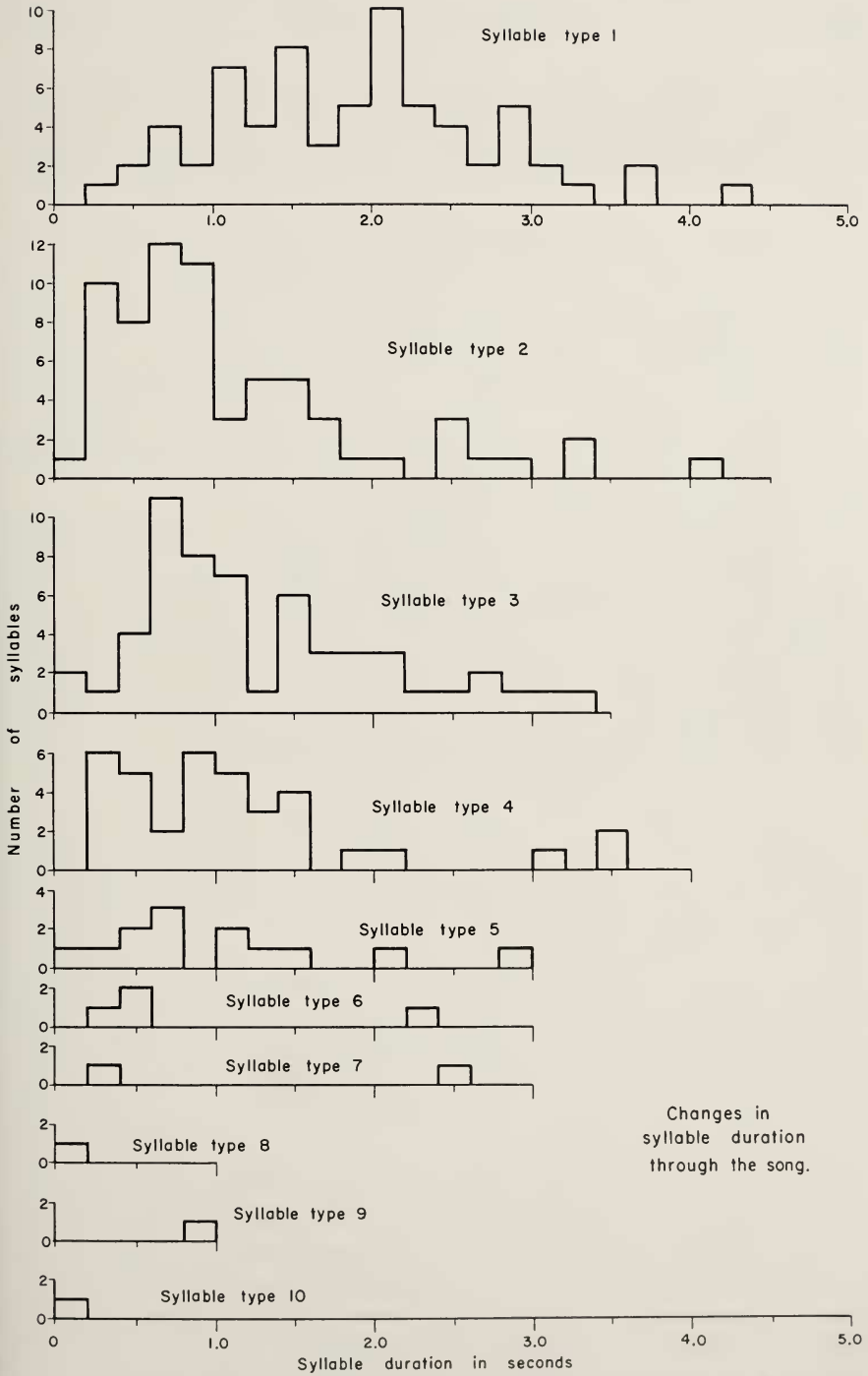

FIG. 5. Frequency distributions of changes in syllable duration by syllable type sequence through the song.

discussed (Table 1). There is usually a trill at the start of a song (in 56 of 67 songs), but apart from this the positions are irregular. Thus, there are often trills in the middle of a song (in 42 of 67 songs) and at the end (in 36 of 67 songs). The phrases are also distributed in rather irregular fashion.

The number of syllables which make up a trill seems to be related to its position in the song. The average figure for the first trill in the song is lower than in other parts of the song (1st trill: 3.5 ± 1.7 syllables; other trills: 4.6 ± 2.2 syllables). In spite of this, the first trill is longer than those which follow (0.67 ± 0.16 sec, as compared with 0.55 ± 0.19 sec for the others). The variability is great, but the differences are statistically significant (Table 2). Another possibility is a consistent change in frequency during the song. We could find none, by referring either to the maximum and minimum frequencies, or to the frequency spread.

Measures were also taken of the duration of the syllables through the song. If the duration of the first example of each syllable type is measured, the first syllable in the song proves to average consistently longer than those which follow (Fig. 5). If we treat phrase and trill syllables separately we can show that the latter are mainly responsible for this trend, those in the first position averaging about twice as long as those in the second, third, and fourth positions (0.19 ± 0.07 sec for the first trill syllable as compared with 0.10 ± 0.06 sec for the second, and so on; see Table 2).

STRUCTURE OF SINGLE SYLLABLES AND NOTES

The analysis so far has failed to account for the impression of extreme variability which the songs of these Mexican Juncos convey. Although the pattern of trills and phrases is varied, it is in the structure of the component notes and syllables that we find the greatest diversity. In an attempt to describe this structure more adequately we took separate tracings of the notes in each syllable type. Various attempts to classify the 497 notes resulted finally in a division into two classes, vibrato and non-vibrato notes. These in turn were subdivided according to the type of frequency inflection: whether rising, falling, steady, rising and then falling, or falling and then rising. A selection of typical examples is presented in Fig. 6 to illustrate the variability of note structure. Only eight of the ten possible classes are shown because two did not occur (non-vibrato: steady; and vibrato: falling and then rising). There were about three times as many non-vibrato as vibrato notes (378:117). Within each group some types are more common than others (Fig. 6, legend) but the diversity is nevertheless the most impressive aspect. There is no particular note type which predominates sufficiently over all other types that it could be said to characterize the song.

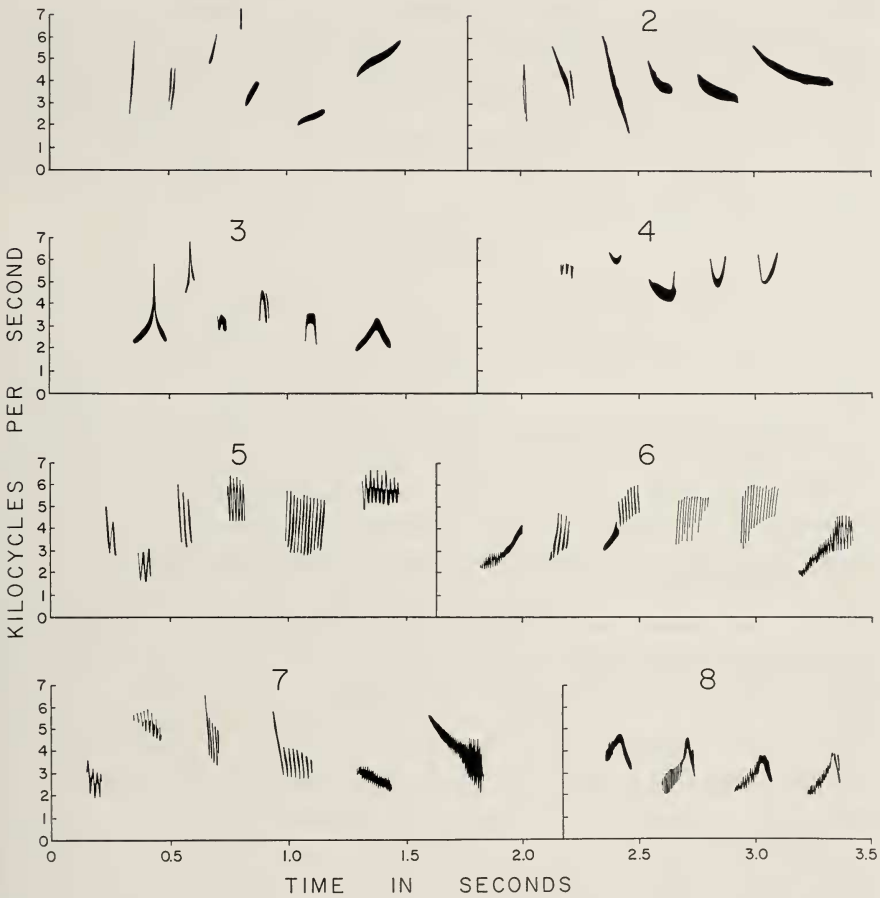

Fig. 6. Note types selected from various songs: The percentage which each note type contributes to the total is given in parentheses. 1 to 4—non-vibrato: (1) upward inflected (17.9), (2) downward inflected (25.2), (3) upward then downward inflected (26.2), (4) downward then upward inflected (6.8). 5 to 8—vibrato: (5) not inflected (10.3), (6) upward inflected (5.2), (7) downward inflected (7.6), (8) upward then downward inflected (0.8).

We also examined the way in which notes are organized into syllables. By recording the number of notes per syllable from which each individual note of the sample had been drawn, we found that vibrato notes come from syllables with fewer notes (2.0 ± 0.8 per syllable) than the non-vibrato notes (2.7 ± 1.2 per syllable, a significant difference: Table 2). Apart from this, each note type is equally likely to occur in a long syllable as in a shorter one. All types are also equally likely to occur at the beginning, middle, or

end of the song. Nor is there any difference in the occurrence of note types in the syllables which are formed into trills and those which form phrases. However, the number of notes in trill and phrase syllables differs significantly (1.5 ± 0.8 notes per phrase syllable, 2.4 ± 1.1 per trill syllable; Table 2). There is also a separate relationship with the position of the syllable in the song. It has already been pointed out that syllable duration is greatest at the start of the song (Fig. 6).

DISCUSSION

The variability of Mexican Junco song.—Detailed physical analysis has done little to dispel the initial impression gained by listening to songs of Mexican Juncos in the field. There is a remarkable degree of variability from individual to individual, even within a single population. The properties which the songs of all individuals within this sample tend to have in common, on the average, are: a certain duration, and a selection of from two to five syllable types, with at least two and sometimes three of these repeated several times to form trills, giving a total of about ten syllables per song. Syllables are about 0.14 seconds in duration, although syllables in the first trill are rather longer than those in later trills. The variability of some of the other properties of the song is very striking. The trills are organized in a more regular fashion than the phrases. Nevertheless, the trills may appear in any part of the song, at the beginning, in the middle, or at the end, and the position of the loudest syllables is similarly irregular. The frequency characteristics vary widely, and there is no consistent pattern of frequency change through the song. Above all, there is great variability in the structure of the notes from which the syllables are built up.

Compared with some of the other emberizine finches, there is no doubt that Mexican Junco song is excessively variable in some respects, at least in this part of the range. The variability is probably less extreme than in songs of some of the more versatile singers, such as certain thrushes. Few quantitative studies of variation in bird song have yet been made, so that precise comparisons are difficult. Detailed syllable structure has proved to be variable in several species such as the Rufous-sided Towhee, *Pipilo erythropthalmos* (Borror, 1959*a*), the Brown Towhee, *Pipilo fuscus* (Marler and Isaac, 1960*b*), and the Chipping Sparrow, *Spizella passerina* (Borror, 1959*b*; Marler and Isaac, 1960*a*), and it may be that the Mexican Junco is a typical emberizine in this respect. The much simpler song of the Oregon Junco (*Junco oreganus*) is also variable in syllable structure, even though there is usually only one syllable type per song (Marler, Kreith, and Tamura, in press). Frequency characteristics have proved to be similarly variable in other species.

The variability of the over-all pattern in time is more unusual. The Rufous-sided Towhee has a similar variety of syllable types in each song, but they

are arranged in a fairly regular pattern, so that Borror (1959*a*) can speak of an introduction and a trill. The European Chaffinch also has a variety of syllable types in each song, but they are organized into a series of trills, and an end-phrase (Marler, 1952; Thorpe, 1958). There is no such regularity in the way in which trills and phrases are placed in the songs of Mexican Juncos.

Song recognition.—We have suggested elsewhere that variability in bird songs is unlikely to be accidental, but should be related in some way to the function which a song performs (Marler, in press; Marler and Isaac, 1960*b*). It has been argued that specific and individual recognition, both of which can be mediated by bird songs, will encourage different evolutionary trends, toward stereotyped species-specificity in certain characters, and toward individual variability in others. It is thus of some interest to determine which song characters are shared by all members of a population, and which differ from individual to individual. As we have seen, Mexican Junco songs have many characters which vary consistently from individual to individual, and relatively few which are shared by all members of the population. Moreover, those which are shared are rather vague and indefinite in nature, so that we can only characterize the species-specific qualities of the song in an approximate way. We are thus led to ask what qualities are used by the juncos themselves in specific recognition. A final answer can only be given to this question by experiments, which would have to take into account the songs of other birds in the area, with which there might be confusion. The avifauna in the pine woods around El Salto is a simple one, occupying extensive uniform areas. The small number of bird species present may be a factor in determining the lack of highly stereotyped species-specific characters in junco song. This appears to be the case on some small islands, where an increased variability of songs as compared with the mainland populations can sometimes be correlated with the reduced avifauna, which simplifies the problem of specific song recognition (Marler, 1960).

There is an abundance of characters to permit individual recognition by song, even for a human observer. It would be interesting to know the developmental basis of these individual characteristics. Juncos living together in a group sometimes shared resemblances in syllable structure which could have a learned basis or a genetic one. The study of song development in captive-raised birds, which we plan to make in the future, will help us to decide between these two alternatives.

SUMMARY

The songs of 63 male Mexican Juncos living together in the same population, in Durango, Mexico, proved to be very variable in many characteristics. The average duration is 1.63 ± 0.29 seconds. The number of syllable types per song pattern usually

ranges from two to five. Syllables average 0.137 ± 0.087 second in duration, with the first in the song tending to be longer than those which follow. Some syllables are given singly, others are repeated in trills. The position of the trilled parts of the song, of which there are usually two, sometimes one or three, is very variable. The average number of syllables per song is 10.1 ± 2.9. Most of these occur in the trills which make up the greater proportion of the song, and are the most regular component. The frequency characteristics vary widely. There are no systematic changes in loudness or in tempo through the song, except for a tendency for the first trill in the song to have fewer, longer syllables than those which follow. The individual notes from which the syllables are built up have a wide variety of forms. The species-specific qualities of the songs of this population of Mexican Juncos are less definite and stereotyped than in some other emberizine finches.

ACKNOWLEDGMENTS

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